

Spatial Attention Determines the Nature of Nonverbal Number Representation

Daniel C. Hyde¹ and Justin N. Wood²

Abstract

■ Coordinated studies of adults, infants, and nonhuman animals provide evidence for two systems of nonverbal number representation: a “parallel individuation” system that represents individual items and a “numerical magnitude” system that represents the approximate cardinal value of a group. However, there is considerable debate about the nature and functions of these systems, due largely to the fact that some studies show a dissociation between small (1–3) and large (>3) number representation, whereas others do not. Using event-related potentials, we show that it is possible to determine which system will represent the numerical value of a small number set (1–3 items) by manipulating spatial attention. Specifically, when attention can

select individual objects, an early brain response (N1) scales with the cardinal value of the display, the signature of parallel individuation. In contrast, when attention cannot select individual objects or is occupied by another task, a later brain response (P2p) scales with ratio, the signature of the approximate numerical magnitude system. These results provide neural evidence that small numbers can be represented as approximate numerical magnitudes. Further, they empirically demonstrate the importance of early attentional processes to number representation by showing that the way in which attention disperses across a scene determines which numerical system will deploy in a given context. ■

INTRODUCTION

We allocate an enormous amount of time and significance to numbers—for example, we count votes to determine our political leaders, portion chemicals to create life-saving medicines, and add up costs to calculate the family budget. Studies with nonhuman animals, human infants, and human adults across disparate cultures provide evidence for two core, evolutionarily ancient systems that support our ability to engage in numerical tasks (e.g., Feigenson, Dehaene, & Spelke, 2004; Pica, Lemer, Izard, & Dehaene, 2004; Feigenson, Carey, & Hauser, 2002; Brannon & Terrace, 1998). The “parallel individuation” system operates by selecting and retaining information about objects or groups of objects. It contains information about numerical identity because objects are stored as distinct individuals in working memory, allowing the observer to match stored objects with visible objects in the scene, compare on the basis of one-to-one correspondence, and detect a numerical mismatch. The “numerical magnitude” system operates by establishing a representation of the approximate numerical value of a set. These two systems are subject to distinct signature limits: Parallel individuation has a *capacity limit*—it can represent only up to three to four items at once—whereas numerical magnitude representation has a *ratio limit*—error in the representation of number grows linearly with the size of the set being rep-

resented. Evidence for these signature limits comes from both behavioral and neural investigations. For example, Hyde and Spelke (2009, 2011) have identified neural mechanisms that are sensitive to the same limits that have been identified in behavioral studies: An early-evoked component (N1) modulates by absolute number with small, but not large, number arrays, whereas a later-evoked component (P2p) modulates by the ratio difference between arrays for large, but not small, numbers. To date, however, there is extensive debate regarding the nature, function, and specialization of these systems for representing small and large numbers.

Some experimental findings suggest small numbers of items (1–3) are represented exclusively through parallel individuation as distinct individuals, whereas the numerical magnitude system is specialized to represent large numbers of items (4 and above) (reviewed by Feigenson et al., 2004). In contrast, many formal models of numerical representation do not distinguish between the representation of small and large quantities, and propose that both small and large quantities are represented using the numerical magnitude system (Gallistel & Gelman, 2000; Dehaene & Changeux, 1993; Gallistel, 1990; Meck & Church, 1983). There is evidence supporting both positions, which has led to considerable disagreement regarding the most appropriate model of nonverbal numerical cognition. Why does the brain sometimes represent small and large quantities alike and other times represent them differently? Answering this question would not only shed light on the functions of

¹Harvard University, ²University of Southern California

these systems by revealing which situations and tasks elicit their representations but also reconcile a huge body of seemingly contradictory empirical evidence.

In many contexts, small numbers of items (1–3) are represented differently than large numbers. First, in the phenomenon referred to as “subitizing,” human adults can enumerate a small number of objects (on average about 3–4 items) quickly and without error, but performance becomes increasingly slower and error-prone with larger numbers (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008; Trick & Pylyshyn, 1994; Mandler & Shebo, 1982). Second, infants and nonhuman animals can represent up to three to four objects in a set at once, provided that the objects move and are hidden one at a time (Barner, Wood, Hauser, & Carey, 2008; Feigenson & Carey, 2003, 2005; Feigenson et al., 2002). Third, studies using a looking-time procedure show that under the same conditions in which infants successfully discriminate between sets containing large numbers of items (i.e., 4 vs. 8, 8 vs. 16), they fail to discriminate between sets containing small numbers of items that differ by the same numerical ratio (i.e., 1 vs. 2, 2 vs. 4) (e.g., Wood & Spelke, 2005b; Lipton & Spelke, 2003, 2004; Xu, 2003). These patterns of data in adults, infants, and nonhuman animals suggest that parallel individuation may be specialized to represent small numbers of items (1–3), whereas the numerical magnitude system represents larger numbers of items (4 and above).

Other evidence, however, contradicts this view. Studies with humans and nonhuman animals indicate that, in some contexts, approximate numerical magnitude representations can be defined over sets containing small numbers of objects (e.g., Beran, 2007; Cantlon & Brannon, 2006; Call, 2000; Whalen, Gallistel, & Gelman, 1999). For example, Brannon and Terrace (1998) showed that rhesus monkeys can apply an ordinal rule learned with small numbers, one to four, to a novel set of larger numerical values, five to nine, outside of the training range, which indicates that the monkeys represented both the small and large quantities with the same numerical magnitude system. Similarly, in human adults, Cordes, Gelman, and Gallistel (2001) reported that variability in the mental representation increases with number for both small and large numerosities when counting is inhibited and subjects are required to tap out certain numerical values with their finger. Finally, a recent infant study revealed that discrimination of quantities across the small and large number boundary is possible when the ratio between the numbers is increased from twofold (2 vs. 4 failure) to fourfold (2 vs. 8 success; Cordes & Brannon, 2009).

Thus, in some contexts, small numbers of items are represented as distinct individuals using parallel individuation, and in other contexts, small numbers of items are represented as an approximate numerical value using a numerical magnitude representation. How can these seemingly contradictory patterns of results be reconciled?

There is growing evidence for a relationship between number representation and spatial attention, which raises

the possibility that spatial attention plays a role in whether small numbers of items will be represented as distinct individuals using parallel individuation or as an approximate numerical value using a numerical magnitude representation. Specifically, the parallel individuation system has a limit of three to four items, which corresponds to the limit on the number of independently moving objects that can be attended to (tracked) at one time (Scholl, 2001) and to the limit on the number of rapid serial visual presentation (RSVP) streams that can be attended to (monitored) at once (Fougnie & Marois, 2006). Furthermore, neuroimaging studies show that differences between how small and large numbers are processed occur during early stages of visual processing, at the level of spatial attention (Hyde & Spelke, 2009; Ansari, Lyons, van Eimeren, & Xu, 2007; Libertus, Woldorff, & Brannon, 2007). Finally, behavioral studies requiring subjects to enumerate multiple overlapping sets of objects show a limit in the number of sets that can be attended and, subsequently, remembered accurately (Halberda, Sires, & Feigenson, 2006). This behavioral and neurophysiological evidence suggests that spatial attention is related to nonverbal numerical processing. Yet, from this evidence alone, it is unclear what specific role spatial attention plays in number representation.

Psychophysical studies of object-based attention provide evidence that when viewing small numbers of objects (3–4 objects), attention can select each object individually and in parallel (e.g., Pylyshyn & Storm, 1988). However, as the number of objects in a scene increases and exceeds the three- to four-item limit of object-based attention, attention disperses across the scene more broadly, such that multiple objects are selected within the same attended region. When attention spreads over a set of objects in this manner, the visual system automatically forms a statistical or *ensemble* representation of that set, which includes information about the average properties of the objects within the set. For example, under conditions in which objects are crowded together and cannot be selected individually with attention, observers can still reliably estimate the average orientation of the objects within the crowd (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). Ensemble representations can include a wide range of information including the average color, size, location, orientation, and shape of the objects within a set (Alvarez & Oliva, 2008, 2009; Haberman & Whitney, 2007; Chong & Treisman, 2003; Ariely, 2001). Importantly, ensemble representations also include information about the approximate number of items within the set (Halberda et al., 2006). Thus, numerical representation through parallel individuation might occur when attention selects each object individually, whereas numerical representation through the numerical magnitude system might occur when attention spreads over a group of objects and the visual system forms an ensemble representation of the objects included within that attended region. To test these predictions directly, we manipulated how attention distributes across a scene containing small numbers of objects (1–3) and

measured the effects of these manipulations on established ERP components that have previously been linked to these two systems of numerical representation (Hyde & Spelke, 2009).

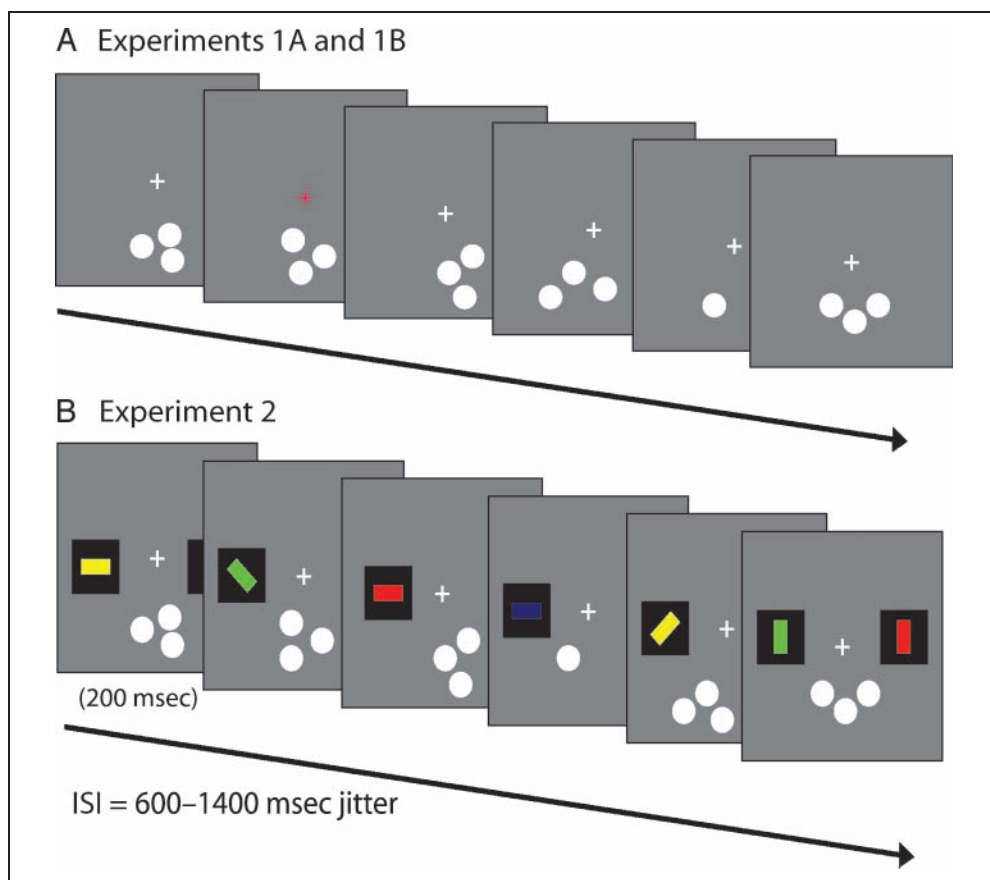
In Experiment 1, we took advantage of the fact that the spatial resolution of attention is much coarser than that of vision—for example, if an observer’s viewing angle of an array of items is reduced sufficiently, they lose the ability to individuate or select the items with attention, but maintain the ability to visually resolve those items (see Intriligator & Cavanagh, 2001; He, Cavanagh, & Intriligator, 1997). Thus, reducing the viewing angle of an array of objects can eliminate the ability to select individual items with attention, even when the number of items is within the capacity limit of visual attention. We used this technique to manipulate how attention dispersed across the scene by varying whether small numbers of objects (1–3) were presented within or beyond the spatial resolution of attention (see Figure 1A).

In Experiment 2, we manipulated attention directly by using a dual-task procedure. In one condition (*high attentional load condition*), participants viewed arrays of one, two, and three dots in the lower visual field while concurrently looking for a target in two RSVP streams (Figure 1B) (Fougnie & Marois, 2006). In a second condition (*low attentional load condition*), participants viewed the same dot arrays and RSVP streams but were not instructed to

look for a target in the streams. Thus, in the first condition, but not in the second condition, participants needed to attend to the particular features of individual items in the RSVP streams.

In both experiments, the images were presented in the lower visual field within a number adaptation-type paradigm (Hyde & Spelke, 2009; Izard, Dehaene-Lambertz, & Dehaene, 2008; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Specifically, a majority of the arrays contained the same number of dots (adaptation number); occasionally, embedded within the stream, a test array was presented that either contained the same number of dots or a different number of dots. The logic behind the number adaptation paradigm is that by habituating the brain to one number and then presenting a change in number, one can identify signatures of the neural mechanisms that process numerically relevant information (see Piazza et al., 2004). To ensure that resulting responses were based on the number of objects in the scene as opposed to non-numerical properties, images were carefully constructed so as to control for continuous parameters other than the number of dots (Hyde & Spelke, 2009; Dehaene, Izard, & Piazza, 2005; Piazza et al., 2004; Xu & Spelke, 2000). Crucially, the paradigm has been shown to elicit neural signatures of approximate numerical magnitude representation (Izard et al., 2008; Piazza et al., 2004) and parallel individuation (Hyde & Spelke, 2009).

Figure 1. Schematic depiction of stimuli presented to subjects. (A) In Experiments 1A and 1B, numerical arrays were presented in the lower visual field as subjects completed a change-detection task at fixation. (B) In Experiment 2, numerical arrays were presented in the lower visual field as RSVP streams of color-bar orientation combinations were presented to the left and right of fixation.



To test whether these attentional manipulations cause small numbers of objects to be represented as discrete individuals or as an approximate numerical magnitude, we analyzed the evoked electrophysiological response to the occasional test images embedded within the stream of adaptation images. Analyses focused on two components known to be implicated in numerical processing: N1 and P2p.

N1 is an early-occurring component, peaking around 150 msec, in response to most visual stimulation (see Luck, 2005 for a review). Several recent studies of numerical cognition report early electrophysiological differences in N1 modulation between small and large numbers in both passive viewing and active numerical comparison tasks (Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998; Dehaene, 1996). More specifically, N1 scales with the number of objects presented to subjects regardless of the adaptation number for small, but not large, numbers of objects (Hyde & Spelke, 2009). The N1 is certainly not a “number-specific” ERP component as it has been repeatedly shown to be modulated by spatial attention in a variety of paradigms and contexts (see Luck, 2005; Hillyard & Anllo-Vento, 1998; Hillyard, Mangun, Luck, & Heinze, 1990). For example, N1 is enhanced for an object that appears in a cued location versus a noncued location (e.g., Hillyard, Luck, & Mangun, 1994). Other studies show that when subjects view stimuli in both visual fields, but are told to attend to and detect a target in just one of those fields, there is an enhanced N1 response for target stimuli appearing in the attended field compared to the non-attended field (e.g., Gomez Gonzales, Clark, Fan, Luck, & Hillyard, 1994). This work suggests that the N1 is a marker of the distribution of spatial attention to objects.

P2p is a mid-latency component, normally peaking around 250 msec over posterior parietal sites, which is modulated by numerical change in a variety of experiments. For example, in both symbolic and nonsymbolic number comparison tasks, P2p shows the classic “distance effect”; the P2p is more positive for close numerical comparisons (i.e., categorizing 6 as larger than 5) compared to more distant numerical comparisons (i.e., categorizing 9 as greater than 5) (Libertus et al., 2007; Pinel, Dehaene, Rivière, & LeBihan, 2001; Temple & Posner, 1998; Dehaene, 1996). Furthermore, a recent study showed that during passive viewing of nonsymbolic numerical arrays in an adaptation paradigm, P2p was sensitive to the ratio difference between the adaptation and test numbers, rather than the exact cardinal value of a given array (Hyde & Spelke, 2009). Using ERP source modeling and fMRI, numerical effects on P2p have been localized to regions of the intraparietal sulcus, a region hypothesized to be selective for number representations (Pinel et al., 2001; Dehaene, 1996). Whether or not the P2p is number-specific, these previous studies suggest that P2p is a good marker of approximate numerical magnitude processing, as it modulates in accord with behavioral signatures of number representation and it appears to originate from number sensitive

brain regions (see Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998; Dehaene, 1996).

If spatial attention determines the nature of nonverbal numerical representation, then under experimental conditions in which attention can select individual objects, we should observe sensitivity to number in N1 as attention distributes to individual items. In this case, if attention selects individuals, we may not observe sensitivity to number change in P2p because ensemble representations are not formed when attention selects individual items. In contrast, when attention cannot select individual objects and is forced to include multiple objects within the same attended region, forming an ensemble representation, we should not observe sensitivity to number in N1 because, across all set sizes, attention selects the single set. Rather, we should observe sensitivity to number change in P2p because multiple objects are included within the same attended region, and thus, the resulting ensemble representation should yield different numerical values across the varying set sizes.

EXPERIMENT 1A: ERP EXPERIMENT

Methods

Participants

Adult subjects from the greater Cambridge, MA, community were recruited through a Web-based study pool. The project was approved by the Committee for Use of Human Subjects at Harvard University. All subjects provided informed consent and were given either course credit or \$15 for participating. The final ERP dataset consisted of 32 subjects between the ages of 18 and 30, 16 in each viewing condition. The data from seven additional subjects were excluded from the final analyses because of too few test trials for reliable analysis after detection and rejection of artifacts ($n = 6$) and excessive electrical noise ($n = 1$).

Procedure

Subjects were instructed to fixate on a cross in the middle of the computer screen and to push a button as quickly as possible when that cross changed from white to pink. While performing this task, images consisting of white dots were presented in the periphery in the bottom half of the computer screen. In order to encourage fixation, participants were explicitly instructed not to make eye movements toward or look directly at these images, and to continue to fixate on the cross. They were not told that the focus of the experiment was the peripheral images or numerical cognition. The fixation cross changed color approximately 10 times per block or about once per minute during the experiment.

Design and Stimuli

Peripheral arrays were presented sequentially for 250 msec in an adaptation paradigm with a random interval of

600–1400 msec between each array (Hyde & Spelke, 2009; Izard et al., 2008; Piazza et al., 2004). During a given block, the majority of the arrays contained the same number of dots (1, 2, or 3 dots). Test arrays appeared every fourth to sixth image within the stream of images; test arrays contained either the same number of dots or a different number of dots. Every subject was adapted to images of one, two, and three dots in separate blocks; within each block, 20 test arrays of one, two, and three dots were presented (60 test images per block/180 test arrays over the entire experiment). Thus, over the entire experiment each participant viewed four different ratio changes: no change (1:1 ratio), small change (2:3 ratio), medium change (1:2 ratio), and large change (1:3 ratio). The no-change condition was presented for each adaptation numerosity (1:1, 2:2, and 3:3) and each ratio change condition was presented both as increasing (e.g., adapt 1, test 2) and decreasing (e.g., adapt 2, test 1) from the adaptation number (see Table 1).¹ Thus, during each experimental session (within resolution and beyond resolution sessions), there were 60 no-change test trials and 40 of each of the three ratio change conditions. To approximately equate the number of test trials between change and no-change conditions, the last six no-change test images presented in each of the three blocks were eliminated from further analysis.

Images were created using an automated program (see Dehaene et al., 2005 for documentation) designed to produce displays that are controlled for continuous parameters other than the number of dots evoking systematic responses on test trials. This method of stimulus control is based on studies examining numerical cognition in infants (Xu & Spelke, 2000) and has been implemented in a number of recent neuroimaging and electrophysiological studies of numerical cognition (e.g., Hyde & Spelke, 2009; Izard et al., 2008; Piazza et al., 2004). Specifically, the extensive parameters (total occupied area and total luminance) varied randomly within a fixed distribution and were equated, on average, across adaptation images, with intensive parameters (individual item size and interitem spacing) necessarily varying with number. In the test displays, the reverse was true: The intensive parameters were equated, whereas the extensive parameters varied across the displays. Importantly, the smallest and largest values of the distribution used for the extensive parameters of the adaptation displays were the smallest and largest values

presented in test images. Thus, all individual continuous values presented in the test displays were presented equally often in the adaptation displays, and were thus equally familiar between the experimental conditions.²

Subjects viewed the images on a computer screen from a distance of 30 cm. Numerical images were presented, on average, 5.5 cm below the fixation point at the center of the screen. The images were presented in the periphery rather than at the fovea because the resolution of spatial attention is markedly worse in the periphery than at the fovea, allowing us to more easily manipulate the ability of attention to select individual items (He et al., 1997). In the *within spatial resolution condition*, the average individual dot size on the test trials was 1.4 cm (ranging from 0.8 to 2.0 cm in diameter on adaptation trials) and the average interitem spacing was 2.6 cm. Previous studies show that under these viewing conditions, spatial attention should be able to individuate the objects (e.g., Intriligator & Cavanagh, 2001). In the *beyond spatial resolution condition*, subjects viewed arrays in which the interitem spacing and the individual item sizes were reduced so as to inhibit the ability to select items individually with spatial attention. The average individual dot size for these test displays was 0.45 cm (ranging from 0.2 to 0.6 cm in diameter during adaptation) and the average interitem distance was 0.65 cm. These parameters were based on pilot testing and previous estimates of the resolution of spatial attention (Intriligator & Cavanagh, 2001). As subjects viewed the displays, we recorded ongoing EEG from 128 scalp locations using a Geodesic Sensor Net (EGI, Eugene, OR). Electrophysiology was recorded at 250 samples per second and band-pass filtered on-line at 0.1–100 Hz.

Data Reduction and Analysis

Data were first low-pass filtered off-line at 30 Hz and segmented into epochs from 200 msec before to 1000 msec after stimulus onset. The data were then subjected to a computer algorithm to detect eye blinks, eye movements, head motion, bad recording channels, and other artifacts. All epochs containing an eye blink, eye movement, motion artifacts, and/or excessive noise were automatically rejected from further analysis. Epochs with more than 10% bad channels were rejected; bad channels in epochs with less than 10% bad channels were corrected using spherical spline interpolation (Junghöfer, Elbert, Tucker,

Table 1. Ratio Change Conditions Presented to Each Subject in Each of the Three Adaptation Blocks

Adaptation Block	Ratio Change Condition			
	No Change	Small Change	Medium Change	Large Change
Adapt 1	1:1	–	1:2	1:3
Adapt 2	2:2	2:3	2:1	–
Adapt 3	3:3	3:2	–	3:1

& Rockstroh, 2000). Participants retaining less than 10 good test epochs per experimental condition after artifact rejection were excluded from the final analysis (Hyde & Spelke, 2009). After artifact rejection and bad channel replacement, epochs were averaged and then referenced to the average reference. Finally, data were baseline corrected to 200 msec before the numerical image appeared.

Based on visual inspection of the grand-average waveform (i.e., the average waveform from all of the conditions), in combination with reported timings and topographies (Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998; Dehaene, 1996), we designated electrode groupings and time frames that best characterized the N1 and P2p. Different topographical patterns evoked by the two components led us to choose slightly different elec-

trode groups for each component (see Figures 2 and 3). The N1 was defined as the adaptive mean amplitude between 95 and 185 msec over central posterior scalp locations (EGI sites 54, 61, 62, 67, 68, 73, 78, 79, 80). Differences in timing of the N1 between participants led us to use the adaptive mean amplitude (the mean response 20 msec before to 20 msec after the peak negative amplitude between 95 and 185 msec for each subject), rather than the traditional mean amplitude (mean amplitude over a fixed time window) in order to better characterize this component across all participants. The timing of P2p between subjects was relatively stable and therefore we defined it as the mean amplitude between 215 and 299 msec over left (48, 52, 53), central (62, 67, 68, 73, 78), and right (87, 93, 99) posterior scalp locations. Crucially, both the timing and electrode

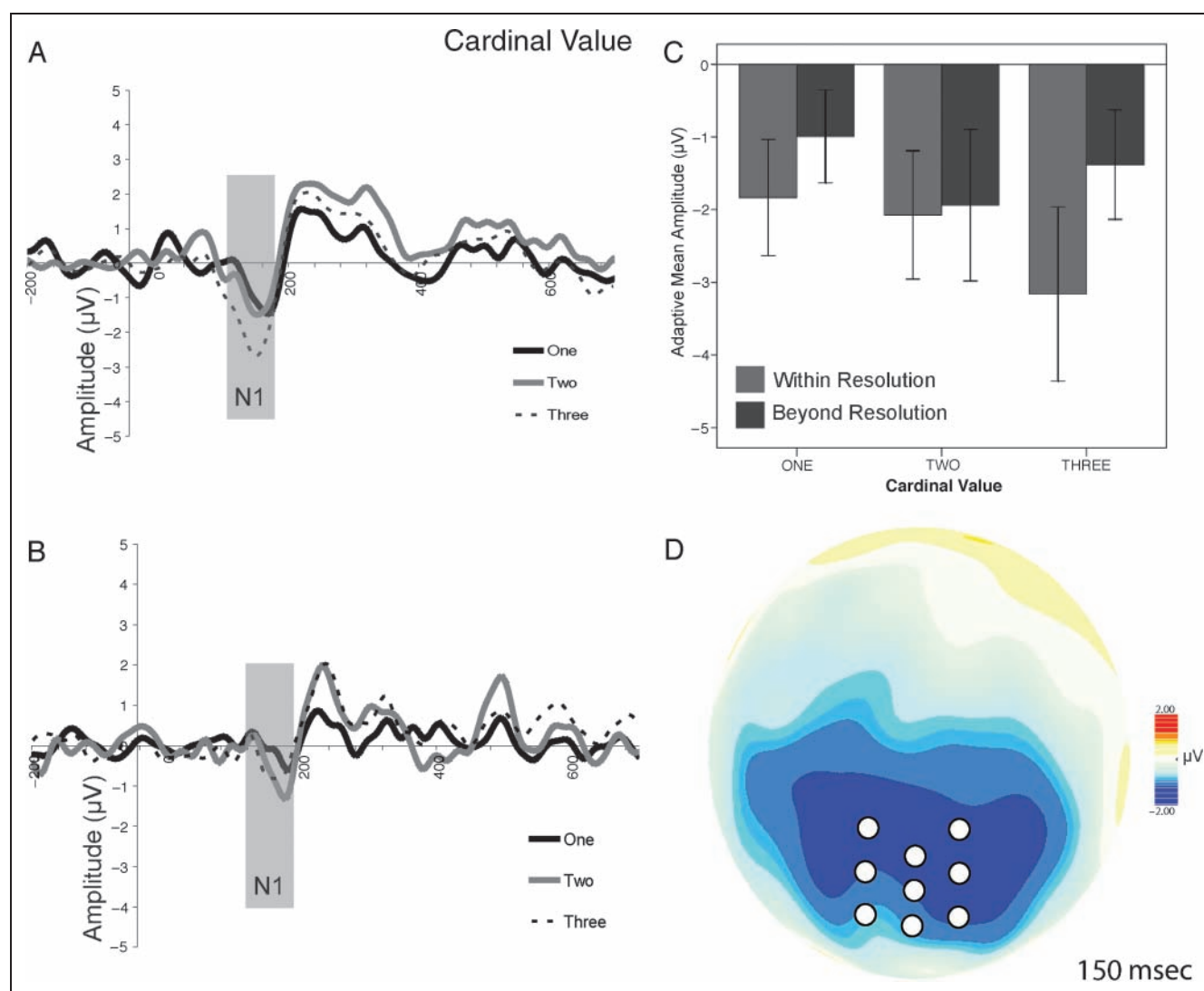


Figure 2. Summary of Experiment 1A ERP findings showing the effect of cardinal value on N1. (A) Average evoked waveform over central posterior sites in response to numbers between 200 and 700 msec in the within spatial resolution condition. The shaded area represents the time window characterizing the N1 (95–185 msec). (B) Average evoked waveform over central posterior sites in response to numbers between 200 and 700 msec in the beyond spatial resolution condition. The shaded area represents the time window characterizing the N1 (95–185 msec). (C) Mean amplitude of the N1 response to cardinal value. Error bars represent 95% confidence intervals. (D) Average scalp topography of the N1 component at 150 msec for both viewing conditions.

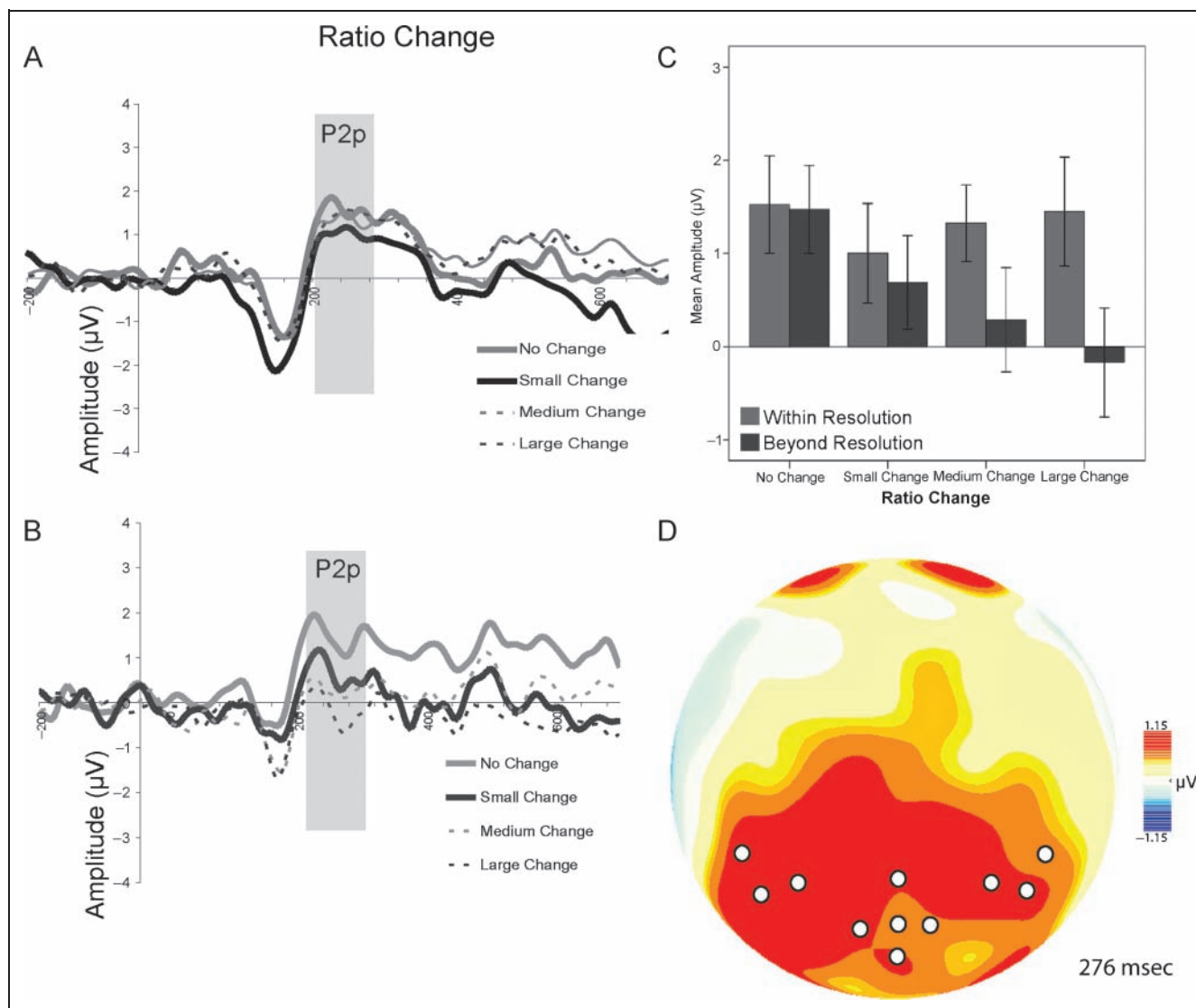


Figure 3. Summary of Experiment 1A ERP findings showing the effect of ratio change on P2p. (A) Average evoked waveform over left, central, and right posterior sites in response to ratio change between 200 and 700 msec in the within spatial resolution condition. The shaded area represents the time window characterizing the P2p (215–300 msec). (B) Average evoked waveform over left, central, and right posterior sites in response to ratio change between 200 and 700 msec in the beyond spatial resolution condition. The shaded area represents the time window characterizing the P2p (215–300 msec). (C) Mean amplitude of the P2p response to ratio change. Error bars represent 95% confidence intervals. (D) Average scalp topography of the P2p component at 276 msec for both viewing conditions.

groupings accord with previous ERP research examining N1 and P2p (Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998; Dehaene, 1996). Analyses were conducted on the mean response over all electrodes selected for a given component. Our primary analyses focused only on the evoked responses to test images containing one, two, and three items within adaptation blocks containing one, two, and three items. ANOVAs were conducted to test main effects and interactions both within subjects and between groups. Post hoc analyses followed up on the main effects and interactions using a test of linear contrast, rather than pairwise comparisons, for the predicted linear pattern of amplitude modulation (Hyde & Spelke, 2009; Ansari, Dhital, & Soon, 2006; Piazza et al., 2004; Pinel et al., 2001).

Greenhouse–Geisser p value corrections (GGp) were applied to any comparison where the assumption of sphericity was violated.

Results and Discussion

We analyzed the effects of the absolute cardinal value of the image (1, 2, or 3 items) as well as the ratio change from adaptation (no change, small change, medium change, large change; see Table 1) under viewing conditions in which the items were spaced within and beyond the resolution of spatial attention (within spatial resolution condition and beyond spatial resolution condition, respectively).

Absolute Cardinal Value (N1)

A mixed-model ANOVA of the adaptive mean of the N1 response with the between-subjects factor of viewing condition (within spatial resolution vs. beyond spatial resolution) and the within-subjects factor of number (1, 2, or 3) revealed a marginally significant effect of viewing condition [$F(1, 30) = 4.14, p < .051, \eta_p^2 = .12$], and a significant interaction between number and viewing condition [$F(2, 60) = 3.33, p < .05, \eta_p^2 = .10$]. Post hoc contrasts for the predicted pattern of N1 modulation revealed a linear trend for the within spatial resolution condition, where N1 increased linearly in magnitude (decreased in amplitude) as number increased [$F(1, 15) = 6.43, p < .05, \eta_p^2 = .30$]. In contrast, in the beyond spatial resolution condition, we observed no systematic modulation based on cardinal value [$F(1, 15) = 0.04, p > .84, \eta_p^2 = .003$] (see Figure 2). These results indicate that in the within spatial resolution condition, the early-evoked N1 response was modulated by the number of objects in the display independent of the ratio change between the adaptation and test numbers. This result replicates previous reports showing that N1 can be sensitive to the number of objects in a scene (Hyde & Spelke, 2009; Libertus et al., 2007).

The N1 response could have been based either on the number of items in the display or on the nonnumerical properties of the display (e.g., surface area) because for the test images, the extensive properties of the display were confounded with number. To distinguish between these possibilities, we compared N1 modulation between the test images and the adaptation images; crucially, for the adaptation images, the extensive properties of the displays were not confounded with number. Thus, if the N1 response was based on the extensive properties of the test displays, then there should be a significant difference in N1 modulation between the test displays and the adaptation displays because extensive properties were confounded in one display type but not in the other. The repeated measures ANOVA with within-subjects factors of number (1, 2, or 3) and image type (adaptation or test) revealed a main effect of number only [$F(2, 30) = 5.96, p < .01, \eta_p^2 = .28$]. The main effect of image type and the interaction were not significant ($ps > .09$). This suggests that the N1 modulation was based on the number of items in the display, not on the nonnumerical parameters of the display in the within spatial resolution condition.

Absolute Cardinal Value (P2p)

A mixed-model ANOVA on the P2p with the between-subjects factor of viewing condition (within spatial resolution vs. beyond spatial resolution) and the within-subject factors of electrode group (left, central, and right parietal) and number (1, 2, or 3) revealed no statistically significant main effects or interactions³ which suggests that the P2p component is not modulated by the number of objects

in the display independent of the ratio change between the adaptation and test numbers.

Ratio Change (N1)

A mixed-model ANOVA with the between-subjects factor of viewing condition (within spatial resolution vs. beyond spatial resolution) and the within-subjects factor of ratio change (no change, small change, medium change, and large change) revealed no significant main effects or interactions (all $ps > .42$). This suggests that N1 did not modulate as a function of the ratio change between the adaptation and test numbers.

Ratio Change (P2p)

A mixed-model ANOVA with the between-subjects factor of viewing condition (within spatial resolution vs. beyond spatial resolution) and the within-subjects factors of electrode group (left, central, and right parietal) and ratio change (no change, small change, medium change, and large change) revealed a significant main effect of ratio change [$F(3, 90) = 3.22, p < .05, \eta_p^2 = .10$], and a significant interaction between ratio change and viewing condition [$F(3, 90) = 2.84, p < .05, \eta_p^2 = .09$]. No other main effects or interactions were significant (all $ps > .2$). Post hoc linear contrasts testing the predicted linear modulation of P2p did not reveal an effect of ratio change in the within spatial resolution condition [$F(1, 15) = .01, p = .92, \eta_p^2 = .001$]. In contrast, a significant linear trend was observed for ratio change in the beyond spatial resolution condition, with P2p amplitude decreasing as ratio increased [$F(1, 15) = 7.42, p < .05, \eta_p^2 = .33$] (see Figure 3).

These results indicate that under conditions in which objects cannot be selected individually with spatial attention, the set of items is represented as an approximate numerical magnitude. This contrasts with the pattern of neural activity observed when the items could be selected individually with spatial attention, in which P2p did not modulate as a function of the ratio change between the adaptation and test displays (see Figure 3).⁴

EXPERIMENT 1B: BEHAVIORAL EXPERIMENT

Next, we examined whether the within and beyond resolution attentional manipulations used in Experiment 1A also influence observers' numerical representations on the behavioral level.

Methods

Nine new subjects (including author D. H.) participated in the behavioral experiment. Subjects viewed the same stimuli as in the ERP experiment and were instructed to maintain fixation and push a button as quickly as possible when either the center cross changed color or the number of dots in the periphery changed. Both reaction time and

accuracy (number of misses divided by the sum of hits and misses) were measured during the session.

Results and Discussion

The ANOVA of the reaction time data with factors of ratio change and viewing condition (within spatial resolution vs. beyond spatial resolution) revealed a significant main effect of ratio change [$F(2, 16) = 50.04, p < .001, \eta_p^2 = .86$]. Post hoc linear contrasts confirmed that reaction time decreased as ratio increased [$F(1, 8) = 107.69, p < .001, \eta_p^2 = .93$] (see Figure 4). Reaction time did not vary significantly between viewing conditions [$F(1, 8) = 3.76, p = .09, \eta_p^2 = .32$].

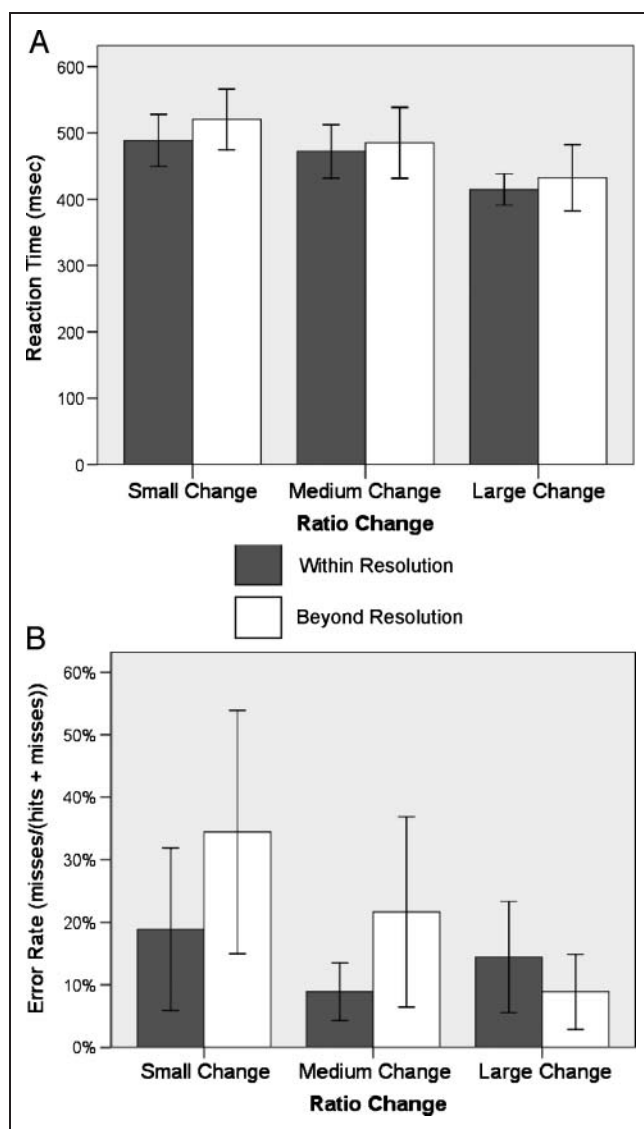


Figure 4. Experiment 1B behavioral results for a number-change detection task using the stimuli from the within spatial resolution condition and the beyond spatial resolution condition of Experiment 1A. (A) Mean reaction times (msec) to number change detection as a function of the ratio of change. (B) Mean error rate (number of misses/sum of hits and misses) for each of the ratio change conditions.

The ANOVA of the accuracy data revealed a significant main effect of ratio change [$F(2, 16) = 4.44, p = .02, \eta_p^2 = .36$], and a significant interaction between ratio change and viewing condition [$F(2, 16) = 4.34, p = .03, \eta_p^2 = .35$]. Post hoc contrasts revealed that accuracy increased as the ratio between the adaptation and test numbers increased when the objects could not be individuated with spatial attention (beyond spatial resolution stimuli) [$F(1, 8) = 9.00, p = .01, \eta_p^2 = .53$], but not when the items could be individuated with spatial attention (within spatial resolution stimuli) [$F(1, 8) = 0.36, p = .56, \eta_p^2 = .04$] (see Figure 4). Thus, participants detected changes involving one, two, and three items with equally high precision and accuracy when the objects could be selected individually with spatial attention, whereas accuracy was modulated by the ratio of numerical change when the objects could not be selected individually with spatial attention.

These results confirm that the stimuli used in the ERP experiment could successfully elicit representations from the parallel individuation system (which enumerates small numbers of items precisely) and the approximate numerical magnitude system (which enumerates items approximately). Furthermore, these results create a link between the contrasting neurophysiological signatures revealed with ERPs and a behavioral measure of the precision of numerical estimation.

EXPERIMENT 2

One limitation of Experiment 1 is that the manipulation of attention was indirect. Specifically, we used different stimuli in each condition to manipulate subjects' ability to select individual objects via spatial attention. Thus, it remains unclear whether the contrasting neurophysiological patterns occurred from manipulations to attention per se or from manipulations to the stimulus properties of the arrays. To distinguish between these possibilities, we directly manipulated attentional load while holding the visual stimulus constant. To do so, we added two RSVP streams to either side of fixation. In the high attentional load condition, observers were instructed to look for a target in those streams while maintaining fixation. In the low attentional load condition, observers did not need to look for a target in those streams. Thus, in the high attentional load condition, observers needed to use attentional resources to detect a target in the streams, thereby leaving fewer attentional resources available to select the objects in the dot arrays.

If the contrasting ERP signatures observed in Experiment 1 were due to the stimulus properties, then in Experiment 2 we should not observe those contrasting ERP signatures because the objects have identical stimulus properties. However, if the contrasting ERP signatures observed in Experiment 1 were due to manipulations on spatial attention, then in the high attentional load condition the ERP signatures should be similar to those observed in the beyond spatial resolution condition in Experiment 1,

and in the low attentional load condition the ERP signatures should be similar to those observed in the within spatial resolution condition in Experiment 1.

Methods

Participants

The data set consisted of 16 new subjects between the ages of 18 and 30 years. Data from one additional subject were excluded from the final analyses because of too few test trials for reliable analysis after detection and rejection of artifacts.

Procedure

Subjects were again instructed to fixate on a cross in the middle of the computer screen and pay attention to the images presented in the periphery. All subjects participated in both high and low attentional load conditions, which contained the same visual stimuli. In the low load condition, subjects were instructed to simply maintain fixation while attending to the visual display. In the high load condition, subjects were asked to monitor two RSVP streams of colored bars, placed to the left and right of fixation, and to push a button when a red vertical bar appeared within either stream. The other objects in the stream consisted of colored bars with different orientations and colors (Fougnie & Marois, 2006). As in Experiment 1, images consisting of varying numbers of white dots were presented in the lower visual field.

Design and Stimuli

The stimuli and design were identical to those used in the within attentional resolution condition in Experiment 1 except in the following ways. First, we increased the number of trials in each experimental session from 40 trials to 52 trials. Second, RSVP streams were presented to the left and right of the fixation cross (8 cm from fixation). The RSVP streams contained rectangular bars with four possible orientations (vertical, horizontal, diagonal left, diagonal right) and four possible colors (red, green, yellow, blue). A new object was presented every 150 msec with an inter-stimulus interval of 50 msec (see Figure 1B). The presentation of these images was offset with the presentation of the adaptation images. Approximately four targets (red vertical bar) appeared at each side randomly during every adaptation block. This means a target appeared in one of the locations about once a minute.

Data Reduction and Analysis

The same parameters for data processing were applied as in Experiment 1. The electrode sites identified in Experiment 1 were used to characterize the N1 and P2p in Experiment 2. However, more prominent and peaked evoked

components were observed, probably as a result of more test trials per condition, leading us to use more restricted time frames to characterize the N1 and P2p compared to Experiment 1 (N1 = mean amplitude between 110 and 150 msec; P2p = mean amplitude between 200 and 250 msec). Our analysis focused on the predicted effects of interest from Experiment 1 (N1 modulation by cardinal value and P2p modulation by ratio). The within-subjects design warranted the use of repeated measures ANOVAs to test for omnibus effects and interactions. Post hoc linear contrasts were run to test for the predicted pattern of results where significant omnibus tests were obtained.

Results and Discussion

Behavioral RSVP Target Detection

Subjects detected 62.5% (standard deviation = 20.7%) of the targets that appeared in either of the two RSVP streams during the high attentional load condition.

Absolute Cardinal Value (N1)

A repeated measures ANOVA on the mean amplitude of the N1 response with the within-subjects factors of attentional load (low attentional load condition and high attentional load condition) and number (1, 2, or 3) revealed a significant main effect of number [$F(2, 30) = 6.54, p < .005, \eta_p^2 = .30$], and a significant interaction between number and load [$F(2, 30) = 3.81, p < .05, \eta_p^2 = .20$]. Post hoc contrasts for the predicted pattern of N1 modulation revealed a linear trend for the low attentional load condition, where N1 increased linearly in magnitude (decreased in amplitude) as number increased [$F(1, 15) = 22.16, p < .001, \eta_p^2 = .60$]. In contrast, in the high attentional load condition, we observed no systematic modulation based on cardinal value [$F(1, 15) = 0.90, p > .35, \eta_p^2 = .06$] (see Figure 5). These results indicate that in the low attentional load condition, the early-evoked N1 response was modulated by the number of objects in the display independent of the ratio change between the adaptation and test numbers. This result replicates previous reports showing that N1 can be sensitive to the number of objects in a scene (Hyde & Spelke, 2009; Libertus et al., 2007) and the results of the within spatial resolution condition of Experiment 1.

Absolute Cardinal Value (P2p)

A repeated measures ANOVA on the P2p with the within-subjects factors of attentional load (low attentional load condition and high attentional load condition), electrode group (left, central, and right parietal), and number (1, 2, or 3) revealed a main effect of electrode group [$F(2, 30) = 6.33, p < .01, \eta_p^2 = .30$], and a three-way interaction between attentional load, electrode group, and number [$F(4, 60) = 2.57, p < .05, \eta_p^2 = .15$]. To follow up

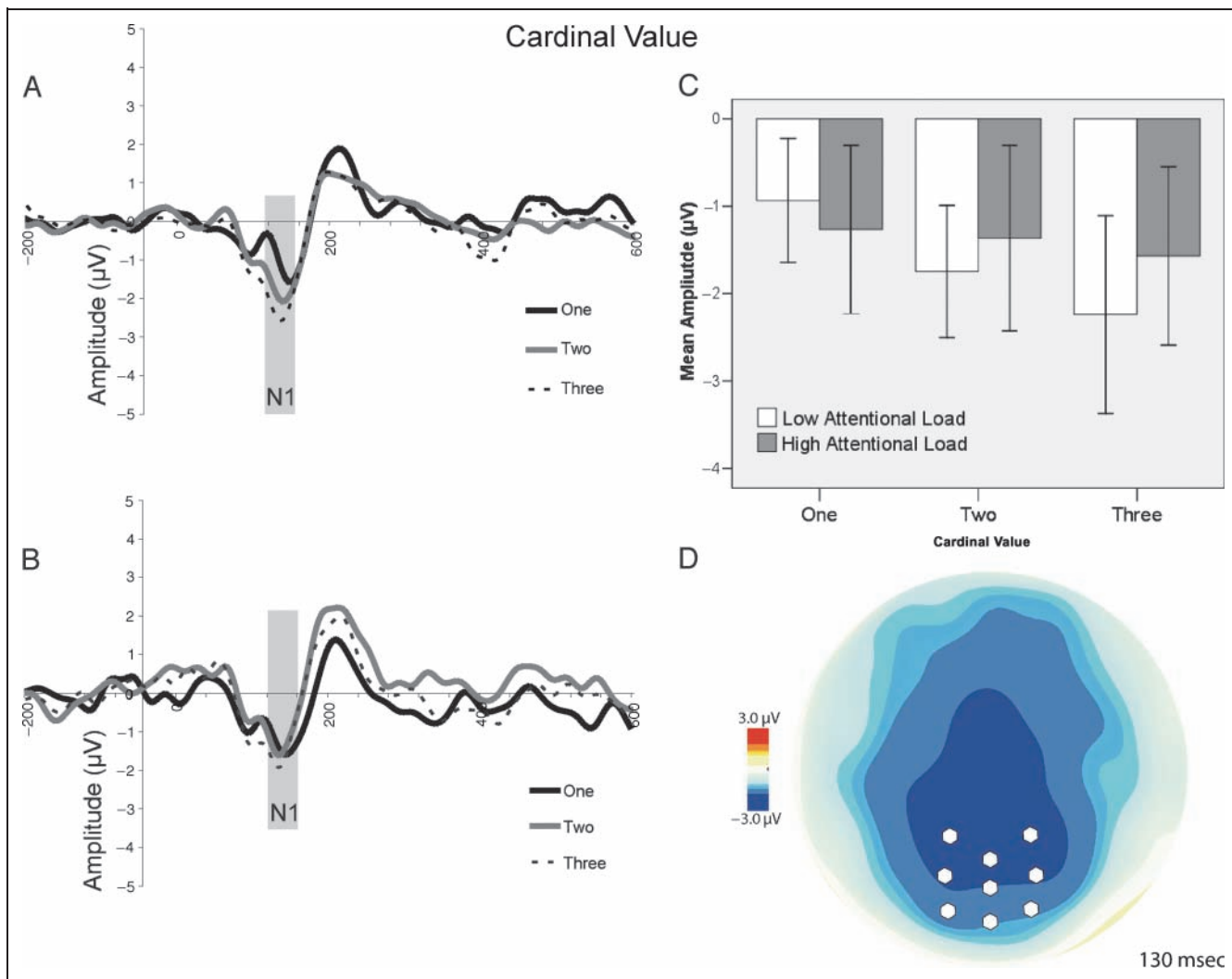


Figure 5. Summary of Experiment 2 ERP findings showing the effect of cardinal value on N1. (A) Average evoked waveform over central posterior sites in response to number between -200 and 600 msec in the low attentional load condition. The shaded area represents the time window characterizing the N1 (110 – 150 msec). (B) Average evoked waveform over central posterior sites in response to number between -200 and 600 msec in the high attentional load condition. The shaded area represents the time window characterizing the N1 (110 – 150 msec). (C) Mean amplitude of the N1 response to cardinal value. Error bars represent 95% confidence intervals. (D) Average scalp topography of the N1 component at 130 msec for all conditions.

on the interaction we conducted a repeated measures ANOVA with the factors of electrode group and number separately for each attentional load condition. For the low attentional load condition, a main effect of electrode group was observed [$F(2, 30) = 3.68, p < .05, \eta_p^2 = .20$]. Post hoc tests revealed the central electrode group produced a greater amplitude response compared to the right electrode group [$t(15) = 2.98, p < .01$]. For the high attentional load condition, we observed a main effect of electrode group [$F(2, 30) = 6.35, p < .01, \eta_p^2 = .30$], as well as an interaction between electrode group and number [$F(4, 60) = 2.88, p < .05, \eta_p^2 = .16$]. However, planned linear contrasts revealed that none of these electrode groups showed the predicted linear pattern of response by number in either direction (all $ps > .12$). These results show that P2p was not modulated systematically by the cardinal value of the display in this experiment.

Ratio Change (N1)

A repeated measures ANOVA on the N1 with the within-subjects factors of attentional load (low attentional load condition and high attentional load condition), and ratio change (no change, small change, medium change, and large change) revealed no significant main effects or interactions (all $ps > .08$). This suggests that the N1 component did not modulate by the ratio of change between the adaptation and test numbers in this experiment.

Ratio Change (P2p)

A repeated measures ANOVA with the within-subjects factors of attentional load (low attentional load condition and high attentional load condition), electrode group (left, central, and right parietal), and ratio change (no change,

small change, medium change, and large change) revealed a significant main effect of ratio change [$F(3, 45) = 3.26, p < .05, \eta_p^2 = .18$] and electrode group [$F(2, 30) = 5.51, p < .01, \eta_p^2 = .27$], and a significant three-way interaction between ratio change and attentional load and electrode group [$F(6, 90) = 2.30, p < .05, \eta_p^2 = .13$]. No other main effects or interactions were significant (all $ps > .12$).

A repeated measures ANOVA with the within-subjects variables of electrode group and ratio change was conducted on each attentional load condition separately to follow up on the three-way interaction. For the high attentional load condition, we observed a significant main effect of electrode group [$F(2, 30) = 4.53, p < .05, \eta_p^2 = .23$], and a significant interaction between electrode group and ratio change [$F(3.3, 49.9) = 2.90, p < .05, \eta_p^2 = .16$]. Post hoc linear contrasts testing the predicted linear modulation of P2p were conducted on each electrode group separately, revealing only the central parietal group to show the predicted pattern of linear modulation by ratio [$F(1, 15) = 9.25, p < .01, \eta_p^2 = .38$] (see Figure 6). A repeated measures ANOVA on the low attentional load condition revealed only a main effect of electrode group [$F(2, 30) = 3.98, p < .05, \eta_p^2 = .21$], with no other main effects or interactions (all other $ps > .54$). Post hoc analysis revealed that the central parietal electrode group evoked larger P2p amplitudes compared to the right parietal electrode group [$t(15) = 2.89, p < .05$], and there was no significant difference between the left and central parietal groups ($p > .10$).

These results suggest that when attentional resources are under high demand, small numbers of objects are not individuated with spatial attention; instead, the set of

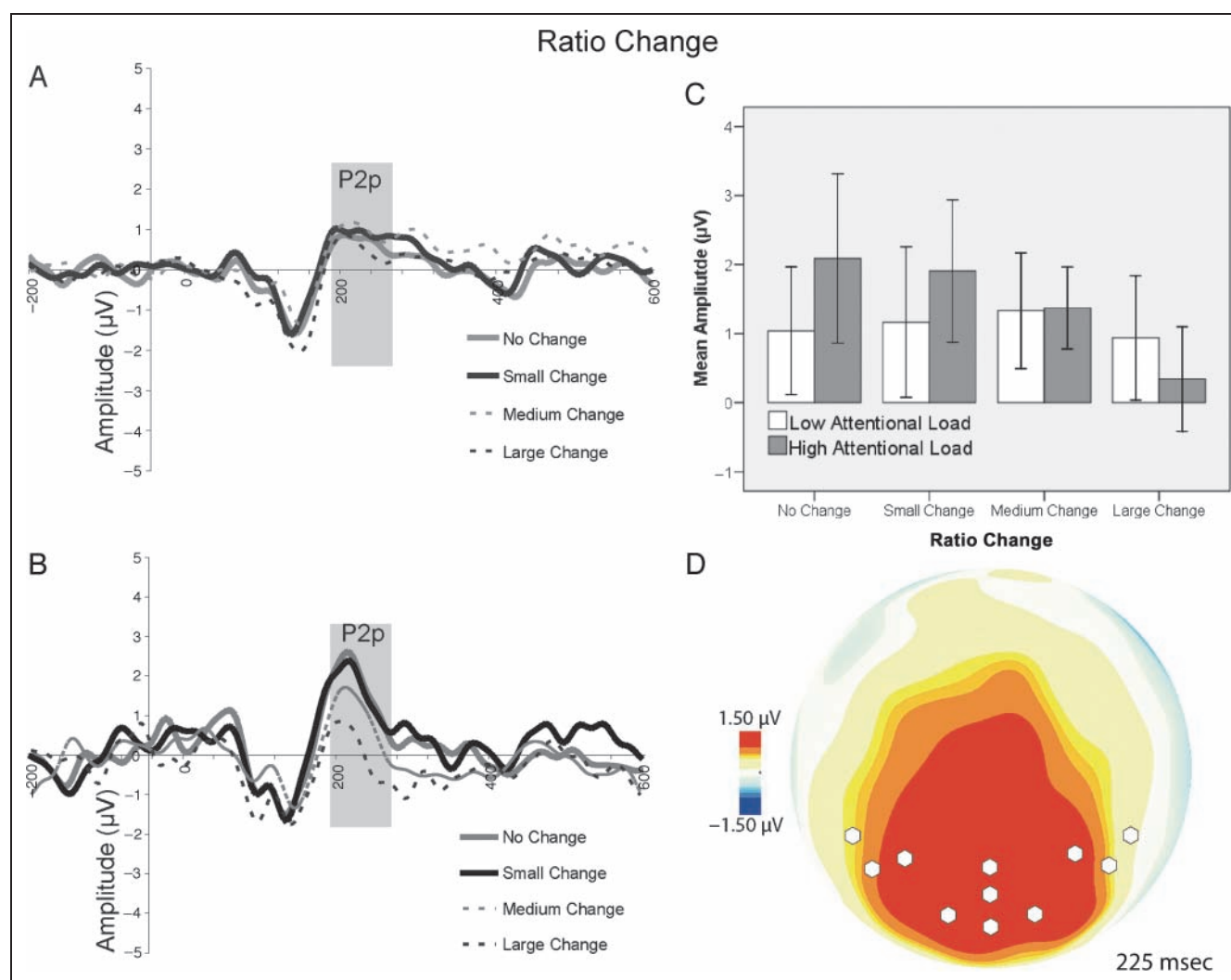


Figure 6. Summary of Experiment 2 ERP findings showing the effect of ratio change on P2p. (A) Average evoked waveform over central posterior parietal sites in response to number between -200 and 600 msec in the low attentional load condition. The shaded area represents the time window characterizing the P2p (200 – 250 msec). (B) Average evoked waveform over central posterior parietal sites in response to number between -200 and 600 msec in the high attentional load condition. The shaded area represents the time window characterizing the P2p (200 – 250 msec). (C) Mean amplitude of the P2p response to ratio change. Error bars represent 95% confidence intervals. (D) Average scalp topography of the P2p component at 130 msec for all conditions.

items is represented as an approximate numerical magnitude. In contrast, when attentional resources are readily available and small numbers of objects can be selected individually with spatial attention, the set of items is represented as distinct objects using parallel individuation (and not as an approximate numerical magnitude). These results replicate those of Experiment 1 under conditions that manipulate directly the availability of spatial attention.

GENERAL DISCUSSION

This study used ERP and behavioral measures to examine the role of attention in the representation of number through parallel individuation and the approximate numerical magnitude system. Our hypothesis was that variations in how spatial attention disperses across a scene determine how a small set of objects will be represented numerically: whether as individual objects or as a set with an approximate numerical magnitude. In Experiment 1, we presented observers with displays containing small numbers of objects (1, 2, or 3) that were spaced either within or beyond the resolution of spatial attention. In Experiment 2, we presented observers with identical visual displays under conditions of low and high attentional loads. When the objects were presented within the resolution of spatial attention and under low attentional load, N1 amplitude increased in magnitude as the number of objects in the scene increased. This converges with previous studies showing that N1 changes as a function of the absolute number of objects in a display for small numbers of objects (Hyde & Spelke, 2009; Libertus et al., 2007). Furthermore, because N1 is classically characterized as a marker of the covert distribution of visual-spatial attention (see Luck, 2005; Hillyard & Anillo-Vento, 1998; Hillyard et al., 1990), we interpret the modulation of N1 to reflect the distribution of spatial attention to individual objects. Importantly, P2p—the neural mechanism associated with numerical magnitude representation—did not vary as a function of the ratio change between the adaptation and test displays under conditions in which items could be selected individually with attention. This indicates that when items are selected individually with attention they appear not to be represented as a group with an approximate numerical magnitude.

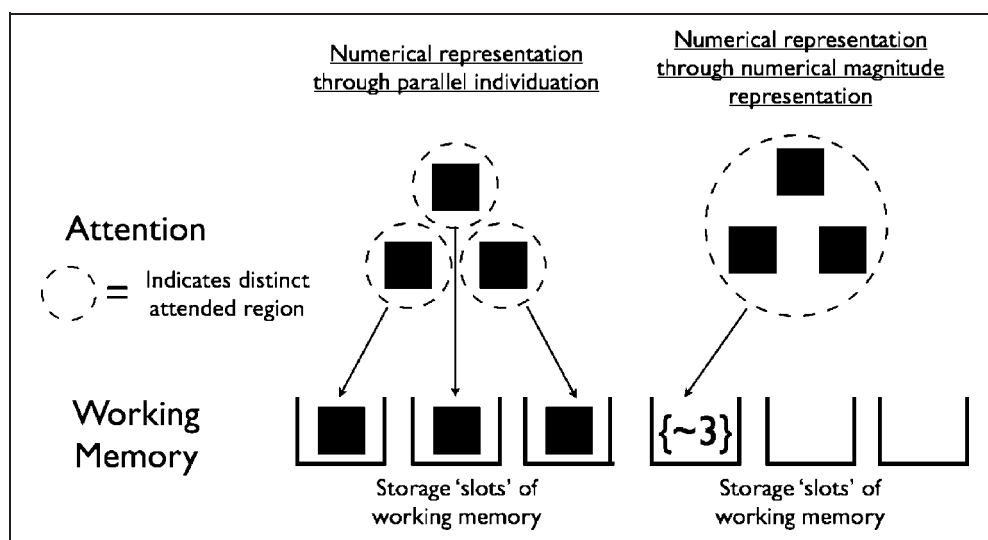
In contrast, when small numbers of objects were presented beyond the resolution of spatial attention or under high attentional load (i.e., attention could not select individual items), we observed no systematic changes in N1 as a function of the number of objects in the scene. This suggests that under these viewing conditions, attention did not distribute to individuals but rather spread over the entire array. Further, we observed evidence of numerical magnitude representation at the later stage in the processing stream: P2p was modulated as a function of the numerical ratio between the adaptation and test displays. Such ratio-dependent brain responses are normally observed when participants are presented with arrays con-

taining large numbers of items (Ansari et al., 2006; Piazza et al., 2004; Temple & Posner, 1998; Dehaene, 1996). The current study provides the first evidence for a ratio-dependent P2p brain response to small numbers (<4), similar to the P2p ratio-dependent brain response observed for large numbers (Hyde & Spelke, 2009). The main difference between the experimental groups in the current study was whether the objects could be selected individually with attention. Thus, when attentional limits do not allow the selection of individual objects, the visual system may be forced to treat the group as a single ensemble representation, with approximate number represented as a statistical property of that ensemble. The current results, therefore, amend the hypothesis that humans have specialized mechanisms for representing small versus large numbers of items. Rather, constraints on our ability to attend to and process stimuli determine the nature of numerical representation.

In the ERP experiments, participants were simply instructed to complete the fixation or the RSVP task and were never told the experiment was about number. Nonetheless, electrophysiological patterns revealed that if items could be individuated, then they were, leading those items to be represented as distinct items rather than as a group with an approximate numerical magnitude. The default, then, may be for small numbers of items to be represented as individuals, provided that those items can be selected individually with attention. Framed in this way, individuation impedes the representation of the approximate numerical magnitude of a small number of items. It is unclear whether this relationship is symmetrical and would work in the opposite direction under appropriate viewing conditions (i.e., whether representing items as a group would impede the representation of those same items as distinct individuals). Further work is needed to determine if, in fact, numerical magnitude representation can impede the parallel representation of individual objects. In addition, future research is needed to determine whether numerical representation is under top-down control. For example, can observers overtly spread their attention over a group of items that are within the spatial resolution of attention, or over a set of sequentially presented items, thereby representing the number of objects in the set as a numerical magnitude representation?

How do these findings fit within the broader framework of numerical representation? Based on the current results, previous studies of ensemble representation in human vision (e.g., Alvarez & Oliva, 2008, 2009; Chong & Treisman, 2003; Ariely, 2001), and studies examining the architecture of numerical cognition (Feigenson, 2008; Halberda et al., 2006), we provide a schematic account of how spatial attention and working memory may interact to determine the nature of nonverbal numerical cognition (Figure 7). When spatial attention can select individual objects, information about each item can be represented as a distinct individual in working memory, with each item taking up a separate “storage slot” (Zhang & Luck, 2008). When this

Figure 7. Proposed model of how spatial attention determines the nature of nonverbal cognition. There are two relevant stages of processing: (1) The distribution of spatial attention across the scene; and (2) the construction of ensemble representations of the statistical properties of the items within an attended region, which can then be stored in working memory. Numerical representation through parallel individuation occurs when attention selects each object individually, and a representation of each object can be transferred into working memory. Numerical representation through numerical magnitude representation occurs when multiple objects are selected within a single region of attention, and an ensemble representation of the statistical properties of the items within the attended region can be transferred into working memory.



occurs, we suggest that observers are representing items using parallel individuation. Thus, the N1 modulation observed in the current study presumably reflects processes that select/determine which items will be represented as distinct individuals in working memory. Although inherently nonnumerical in nature, these representations afford numerical content by retaining information about numerical identity—for example, an observer can match mentally stored objects with visible objects in the scene, compare on the basis of one-to-one correspondence, and detect a numerical mismatch. In contrast, when spatial attention selects a group of objects, information about the items within the group is stored as a single ensemble representation in working memory, with each group/ensemble representation taking up a single storage slot in working memory (Feigenson, 2008; Halberda et al., 2006). When this occurs, we suggest that observers are representing items using numerical magnitude representation. Working memory may therefore retain information about distinct objects and/or groups of objects.

In sum, spatial attention and working memory are both involved in parallel individuation and numerical magnitude representation, and we speculate that the nature in which spatial attention disperses across the scene (i.e., whether individuals or groups are selected) determines (or at least partially determines) how a set of objects will ultimately be represented in working memory.⁵ Of course, our study was not designed to investigate how information is transferred to and stored in working memory. We provide this framework as a guide for future research and to link our findings with those showing that working memory plays a role in numerical representation for both parallel individuation and numerical magnitude representation (Feigenson, 2008; Halberda et al., 2006; Feigenson et al., 2004).

More generally, these results have important implications for understanding how approximate magnitude representations of number are constructed. The fact that they can be formed over small numbers of items when those items are beyond the limits of spatial attention suggests that the construction process does not involve an iterative process in which each item is attended to in series and tagged with the next symbol in the count list (e.g., Gallistel & Gelman, 1992). Rather, these results are consistent with a process that operates over the global properties of the array (Izard & Dehaene, 2007; Wood & Spelke, 2005a; Barth, Kanwisher, & Spelke, 2003).

Most importantly, this study provides a systematic account, which generates clear and testable predictions, of the specific situations that elicit representations of individuals and approximate numerical magnitudes. Number representation through parallel individuation will occur when objects are presented within the capacity and spatial resolution of attention. However, when the objects in a scene are too small, too close together, too far in the periphery to be selected individually, too numerous to be selected simultaneously, or outside demands on attention are too great, attention may disperse over the entire set of objects, leading the visual system to construct an ensemble representation of the number of items in the attended region.

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Reprint requests should be sent to Daniel C. Hyde, Department of Psychology, Harvard University, 1118 WJH, 33 Kirkland Street, Cambridge, MA 02138, or via e-mail: dchhyde@fas.harvard.edu.

Notes

1. Given that the parallel individuation system has a representational limit of three items, it was not possible to orthogonally manipulate ratio and number [i.e., “1” was only involved in medium (1 to 2) or large (1 to 3) ratio changes; “2” was only involved in small (2 to 3) or medium (1 to 2) ratio changes; and “3” was only involved in small (2 to 3) or large (1 to 3) ratio changes]. However, because the two experimental conditions (within attentional resolution and beyond attentional resolution) had identical ratio/number relations, any observed differences in the ERP responses between the conditions cannot be explained by this issue. Similarly, given the restricted capacity of the parallel individuation system, we were not able to test the same ratio changes with other cardinal values in the small number range.
2. Because surface area and contour length are nonlinearly related, it is not possible to control for both nonnumerical variables in a single experiment using visual arrays of identical forms (i.e., controlling for one variable introduces differences in the other). In our study, we elected to control for surface area. However, because the two conditions had identical circumference relations, any observed differences in the ERP responses between the experimental conditions cannot be based on circumference relations.
3. Marginally significant effects of cardinal value [$F(2, 60) = 3.06, p = .054$] and viewing condition [$F(1, 30) = 4.04, p = .053$] were observed. Nonetheless, a test of linear contrast on the marginally significant effect of cardinal value revealed that the response did not pattern linearly as would be predicted if P2p was sensitive to the cardinal value of the display [$F(1, 30) = 2.58, p = .119$] (greatest amplitude P2p was observed for “2”, then “3”, then “1”). Therefore, even though moderate but non-significant differences between conditions were observed, the pattern of P2p modulation was not linear by cardinal value.
4. To test if the N1 and P2p showed number adaptation, we compared the average response to change trials to the no-change trials.
5. At this point, it is unclear whether the P2p ERP component reflects the actual *representation* of numerical information or the *extraction* of information for subsequent visual processes. Nonetheless, the modulation of the P2p in this study and others (e.g., Hyde & Spelke, 2009; Pinel et al., 2001) mirrors the classic distance effect/ratio-dependency observed in behavioral studies of numerical magnitude representation (e.g., Feigenson et al., 2004), suggesting it to be a good marker of engagement by the approximate number system.

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